

THE SKULL OF THE EOCENE *TRIODON ANTIQUUS*  
(TRIODONTIDAE; TETRAODONTIFORMES):  
SIMILAR TO THAT OF THE RECENT  
THREETOOTH PUFFERFISH *T. MACROPTERUS*

James C. Tyler and Colin Patterson

*Abstract.*—The fossil record of the tetraodontiform family Triodontidae previously has been based only on jaw bones. All of these elements are from the early and middle Eocene, and include: numerous unfused premaxillae and fused dentaries for the more commonly recorded *Triodon antiquus* Leriche from several localities in Europe and one in North America; two fused dentaries for *T. cabindensis* Leriche from Africa; and a single dentary for *T. macrognathus* Taverne & Nolf from Belgium. In a monograph on tetraodontiform osteology and relationships, Tyler (1980:260) noted that the presence of *Triodon*-like jaw parts in the Eocene tells us nothing about what the fish behind the jaws was like, and that there was no guarantee that the general form of even the better known *T. antiquus* was at all like that of the only Recent species of the family, the threetooth pufferfish *T. macropterus*. The recovery in 1982 of a specimen of *T. antiquus* from the Lower Eocene London Clay with both the upper and lower jaws attached to a relatively complete skull, along with the cleithra and pelvis, indicates that this Eocene species is similar to the Recent species, especially in the distinctive shapes of the hyomandibular, subopercle, and cleithrum. Examination of a smaller specimen of *Triodon macropterus* than previously available reveals the presence of a posttemporal, a bone thought to be present among tetraodontiforms only in the Balistoidei but lost in the Triodontidae and all of the other Tetraodontoidei.

The family Triodontidae is of special interest because it is clearly the most primitive extant group within the Tetraodontoidei, the more advanced of the two lineages of tetraodontiforms (here and elsewhere, higher categories sensu Tyler 1980). Based on both osteology (Tyler 1962, 1980) and myology (Winterbottom 1974), the Triodontidae is considered the sister group of all of the other tetraodontoid families—the Tetraodontidae, Diodontidae, Molidae, and Eocene Eoplectidae. Triodontids retain many of the primitive features of the Balistoidei, the other major tetraodontiform lineage, including a spiny dorsal fin (although rudimentary and sometimes absent), pelvis, urohyal, dorsal roof of the myodome, com-

plete scapular foramen, a knob on the scapula for support of the uppermost pectoral-fin ray, unsutured actinosts, 12 caudal-fin rays, a generalized caudal skeleton and branchial basket, etc. However, triodontids possess the single most important tetraodontoid synapomorphy—which is the presence of highly modified, non-protruding teeth fully incorporated into the matrix of the premaxillae and dentaries, together forming a complex beak-like structure supported by a massive and firmly sutured palatine-ethmoid-vomerine block.

The Recent Species of *Triodon*

A single species of triodontid is alive today: *T. macropterus* Lesson, benthic in the

Indo-western Pacific from southeast Africa to Japan in depths of 50 to 300 meters (Tyler 1967:90, Kyushin et al. 1977:364, Matsuura 1985:409, Smith 1986:894). The great majority of specimens in museum collections are relatively large adults of between 285 and 480 mm SL (Tyler 1967:90), with a few specimens recorded as large as 540 mm SL (Smith 1986:894) and 550 mm SL (Gloerfelt-Tarp & Kailola 1984:293). Specimens smaller than 285 mm SL have only rarely been reported, such as in Winterbottom (1974:5) for 270 mm SL and in Burgess & Axelrod (1974:1357) for 224 mm SL specimens [the illustration of the 487 mm SL = BL or body length specimen described by Kyushin et al. 1982:299 is incorrectly labeled 103 mm BL; K. Amaoka and K. Matsuura, pers. comm.].

However, trawling by the R/V *Soela* in 1986 off the coast of Queensland, Australia, has procured five relatively small specimens of *T. macropterus* of 89 to 103 mm SL, from depths of 216 to 228 meters. These latter specimens from the Australian Museum are relevant to this study because they are of about the same size as that extrapolated for the Eocene skull of *T. antiquus* described here, allowing comparison of the osteology of fossil and Recent specimens of similar size. This reveals at least one feature not previously known in *T. macropterus*.

### The Fossil Species of *Triodon*

The first described and best known fossil triodontid is *T. antiquus* Leriche (1905:170; description and illustrations repeated with only slight modification in Leriche 1906:266; and further noted in Leriche 1908:3), based only on several premaxillae and dentaries from the early and middle Eocene (Ypresian, Lutetian) of Belgium and France. The teeth were described as small and incisiform, and arranged in superimposed rows incorporated into the substance of the jaw bones, as is the case in both triodontids and diodontids. While the dentaries are ful-

ly fused together in the midline, as in both triodontids and diodontids, the premaxillae are separate, a combination unique to the triodontids. Six premaxillae and ten dentaries of *T. antiquus* were illustrated. One of the dentaries (Leriche 1905, pl. 12, fig. 31) is relatively more elongate (lesser width between the posterolateral rami and more acutely angled at the anteromedial point of the beak) than the others and was given the varietal name *elongatus*. Leriche noted that these Eocene jaw bones are all far smaller than those found in any of the large adult specimens of the Recent *T. macropterus* then available in museum collections, which were about 300 to 400 mm SL. For example, Leriche's illustrated premaxillae of *T. antiquus* are between 11 and 15 mm greatest length and the dentaries between 9 and 12 mm greatest width between the posterolateral rami (anguloarticular processes), whereas in a 391 mm SL specimen of *T. macropterus* the premaxillae are 40 mm long and the dentaries 37 mm wide (this specimen, ANSP 98917, was described and illustrated by Tyler 1980:255, fig. 182, and has been reexamined for this work). Of the five young adult specimens of *T. macropterus* that have become available at the Australian Museum, the 103 mm SL specimen (AMS 25802-006) has been cleared and stained. The premaxillae are 11 mm long and the dentaries 10 mm wide, these figures being at the lower end of the range of these measurements in *T. antiquus*. By extrapolation from the 103 mm SL specimen of *T. macropterus*, the premaxillae and dentaries of *T. antiquus* described by Leriche represent young adult specimens of about 93 to 140 mm SL.

Casier (1946:175) somewhat increased our knowledge of *T. antiquus* by briefly describing and illustrating it on the basis of 24 dentaries and 3 premaxillae from the early Eocene (Ypresian) of Belgium. These jaw bones were even smaller than those described by Leriche, with the illustrated premaxillae being about 5 mm long and the

dentaries between about 3 and 8 mm wide. By extrapolation from the 103 mm SL specimen of *T. macropterus*, these premaxillae and dentaries represent juveniles and young adults of about 31 to 82 mm SL.

Given his familiarity with *T. antiquus*, the report by Casier (1966:374) that this species is absent from the London Clay Formation (Ypresian) of southern England simply indicates that specimens of it had not yet been collected from that formation. We now know that detached dentaries of *T. antiquus* are not uncommon there (see Material), even though a relatively complete skull such as reported here is a rarity.

Some years after his original description of *T. antiquus*, Leriche (1919:480, name only; 1920:85, description and illustration) described *T. cabindensis* on the basis of a single large dentary from the middle Eocene (Lutetian) of Angola at Sassa Zao, Cabinda. The greatest width of this dentary, including an estimate of the missing left posterolateral region, is about 30 mm. The dentary of *T. cabindensis* was said to be relatively wider than in *T. antiquus* and to have the small teeth that are incorporated into the bone lamelliform rather than incisiform. The individual teeth of *T. cabindensis* were illustrated as being about 1.5 mm in width and having about five distinct lobes along the upper edge (toward the mouth). By extrapolation from the 391 mm SL specimen of *T. macropterus*, the type dentary of *T. cabindensis* represents a large adult of about 317 mm SL. A second large dentary of *T. cabindensis*, also of about 30 mm width, was listed, briefly described, and illustrated by Darteville & Casier (1943:91, 1949:253, 1959, pl. 20, fig. 2) from Landana, Cabinda, from the same horizon as the holotype from Sassa Zao.

This additional specimen of *T. cabindensis* became the subject of a detailed and extensively illustrated description and comparison to the holotype dentary of *T. cabindensis* and to the premaxillae and den-

taries of *T. antiquus* by Casier (1960:33–37, pl. 2, figs. 5a–5i), who referred to the additional specimen as “cf. *cabindensis*.” Casier noted a number of superficial and internal differences between the dentaries from Sassa Zao and Landana in the size, form, and ornamentation of the individual teeth in the exposed outer surface of the bone and in the internal trituration plate, and of their relationships with the bony material of the dentary. He found even greater differences between these two large dentaries from Cabinda and the much smaller dentaries of *T. antiquus* from Belgium. He not only questioned whether the dentary from Landana was conspecific with that from Sassa Zao, but, especially since only dentaries were known, whether both were the remains of diodontids rather than triodontids (Casier 1960:35–37).

The only other described species that has been referred to *Triodon* is *T. macrognathus* Taverner & Nolf (1978:147). These authors had two dentaries from the middle Eocene (Lutetian) Lede Formation of Belgium, one of which they referred to *T. antiquus*. The other they described as the new species *T. macrognathus* because of the lesser ornamentation of small individual teeth on the external surface of the beak, the stronger posterolateral wings, and a more slender and distinctly less prominent beak. The illustrations of these two dentaries indicate that the small individual teeth apparent on the outer surface of the dentary in *T. antiquus* are absent in *T. macrognathus*, but the supposed differences in the shape and size of the dentaries are not particularly distinctive to us. The dentary shown for *T. antiquus* is about 5 mm greatest width, and that for *T. macrognathus* about 6 mm wide, corresponding by extrapolation from the 103 mm SL specimen of *T. macropterus* to specimens of, respectively, 52 and 62 mm SL. We remain skeptical about whether the difference between these two dentaries is adequate for specific recognition. Nolf (1970:



113) had previously listed "*Triodon* cf. *antiquus*" from reworked Eocene fossils in the Pleistocene of Merelbeke, Belgium.

The only report of *T. antiquus* from other than Europe is the description and illustration by Weems & Horman (1983:45) of a dentary from the early Eocene (Ypresian) Nanjemoy Formation in Maryland, U.S.A. This dentary is about 10 mm greatest width (as it is also from the anterior midline to the rear of the posterolateral rami) and has small individual teeth with only slightly crenulated upper edges on the outer surface of the beak and several pairs of large trituration teeth internally. These features are all typical of the European specimens of *T. antiquus*, including the type material, which is of similar size to the Maryland dentary (Weems & Horman were mistaken in thinking the Maryland dentary to be larger than most of the European material). The 103 mm SL specimen of *T. macropterus* has a dentary width of 10 mm, and the Maryland dentary thus represents a specimen of *T. antiquus* of very similar size. Weems & Horman (1983:47) noted that the Maryland dentary has a beak that is about as long as wide, whereas in European *T. antiquus* the beak tends to be somewhat wider than long, giving the Maryland beak an especially angular appearance. By contrast, they pointed out that the dentary of *T. cabindensis* is extremely wide (as is that of *T. macrognathus*, a species of which they were not aware). Weems & Horman (1983) were appropriately cautious in their interpretation of the differences in proportions between their Maryland dentary and most European materials of *T. antiquus*, stating that in light of the "highly variable nature of the dentition in figured specimens of *T. antiquus*," the Maryland dentary "is not truly distinctive when based on only a single specimen," and that "unless enough material becomes available to allow a statistical comparison [by size] between the European and American populations," variants like the Mary-

land dentary are "best referred to the highly variable *Triodon antiquus*." We have examined the Maryland dentary and fully support that conclusion.

The new skull of *Triodon* described below and illustrated in Figs. 1–5 is from the Lower Eocene (Ypresian) London Clay Formation. It was collected on the foreshore at Sheppey, Kent, in 1982 by Mr. Brian Gasson of Redhill, Surrey, and was presented by him in 1984 to the British Museum (Natural History). The premaxillae and dentary of this skull, although much abraded, have all the essential characteristics in size and shape and in the form of the exposed tooth structures (e.g., only slight crenulation of the upper edge of the small outer teeth) of the European jaws referred to *T. antiquus*, and we are confident that it represents the same species.

#### Description of the Skull of *Triodon antiquus* Leriche, 1905

The skull as recovered was in a rounded nodule with flat sides (Fig. 1), in which the roof of the cranium, ethmoid-lateral ethmoid-vomerine region, premaxilla, dentary, quadrate, opercular bones, cleithrum and basal region of the pelvis were exposed, affording sufficient clues to its identity as *Triodon antiquus*. Removal of the clay matrix from the right side and top of the skull has exposed the bones of the cheek and snout (Figs. 2–4) and presents further confirmation of the identification, while also indicating the great similarity between the Eocene *T. antiquus* and the Recent *T. macropterus*. The major bones that have been lost from the skull of the London Clay specimen are the frontals, maxillae, articulares, and angulars (and all bones of the pectoral girdle except the cleithra).

The measurements of the skull are: 40 mm from front of upper jaw to rear of supraoccipital (excluding the supraoccipital crest that is abraded away); 35 mm from



Fig. 1. *Triodon antiquus*, BM(NH) P.62702, length from front of upper jaw to rear of supraoccipital 40 mm, left side of skull in matrix as recovered, Lower Eocene, London Clay Formation, Sheppey, Kent. Rule is mm.

front of ethmoid-vomerine block to rear of supraoccipital; 17 mm greatest width across pterotics-posttemporals (edge estimated on posterolaterally incomplete right side); 11 mm greatest width between the posterolateral rami of dentary; 11 mm greatest midline length of dentary (between mid-front of dentary and a line across posterior ends of rami); 11 mm from mid-front of dentary to posterolateral edge of dentary. Two comparable measurements from the 103 mm SL specimen of *T. macropterus* allow for the estimation of the length of the London Clay specimen; 34 mm from the front of the ethmoid-vomerine block to the rear of the supraoccipital (exclusive of the posterior extension of the crest), and 10 mm greatest width between the posterolateral rami of the dentary. By extrapolation from these figures, the London Clay specimen was between 106 and 111 mm SL.

The osteology of the Recent *T. macropterus* previously has been known only on the basis of large adults, especially the two cleared and stained specimens described by Tyler (1962:795, 1980:244, see Tyler 1967:88 for a review of specimens then available for study, including older skeletal materials used by Camille Daresse and Henri Hollard in the mid-19th century). Because the skull of *T. antiquus* from the London Clay obviously represents a much smaller individual than the 391 and 463 mm SL specimens of *T. macropterus* described and extensively illustrated in the literature, we have taken advantage of the recent availability of relatively small specimens of *T. macropterus* at the Australian Museum to clear and stain a 103 mm SL specimen and illustrate dorsal and lateral views of its skull (Fig. 6) for ease of comparison with our reconstructions of the Eocene skull (Fig. 5).



Fig. 2. *Triodon antiquus*, same specimen as Fig. 1, right side of skull with matrix removed. See Fig. 5 for interpretation of bones.

On the dorsal surface of the neurocranium the most clearly delineated bone is the supraoccipital, whose crest is abraded down to its base. The lines of articulation are less

clear between the anterodorsal extension of the exoccipital where it separates the supraoccipital from the epiotic, posttemporal, and pterotic. The frontals, which in the Re-



Fig. 3. *Triodon antiquus*, same specimen as Fig. 1, slightly oblique dorsal view of skull with matrix removed from right side. See Fig. 5 for interpretation of bones.



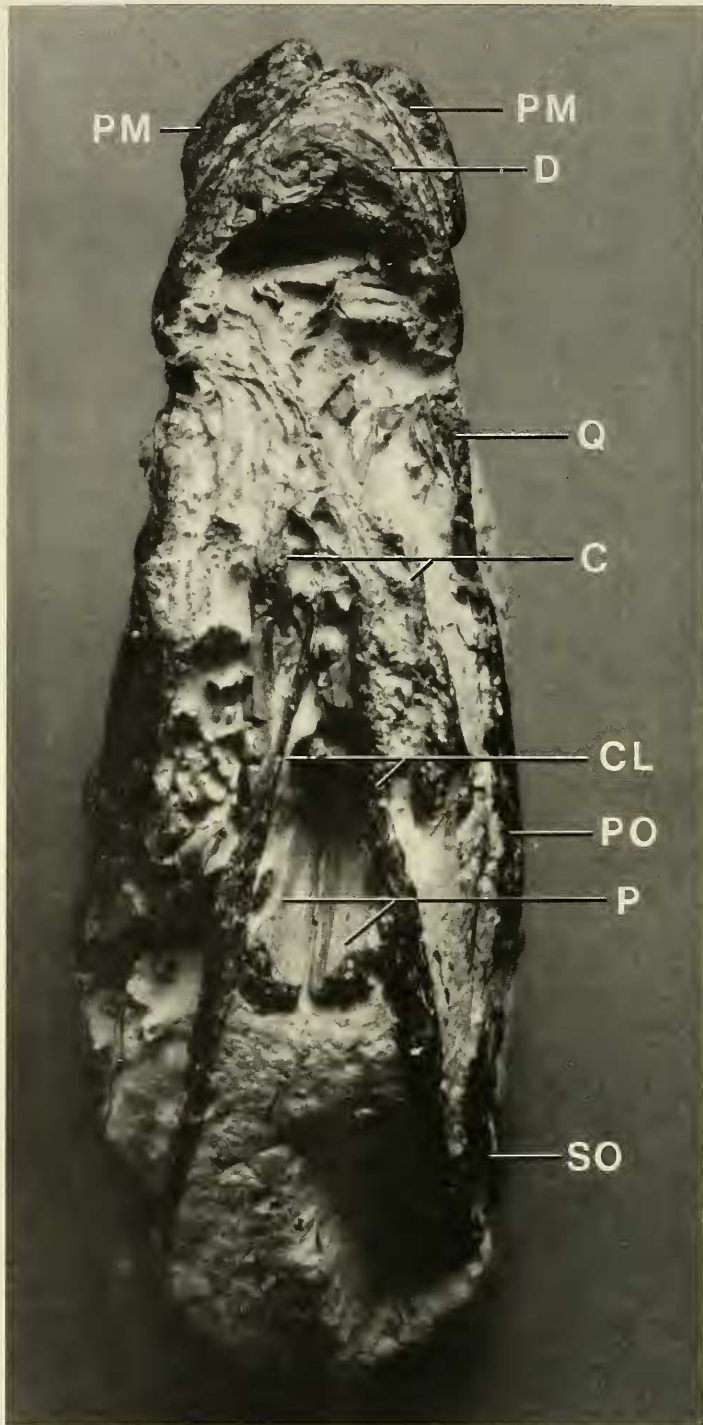


Fig. 4. *Triodon antiquus*, same specimen as Fig. 1, ventral view of skull. See legend for Fig. 6 for explanation of abbreviations of names of bones.

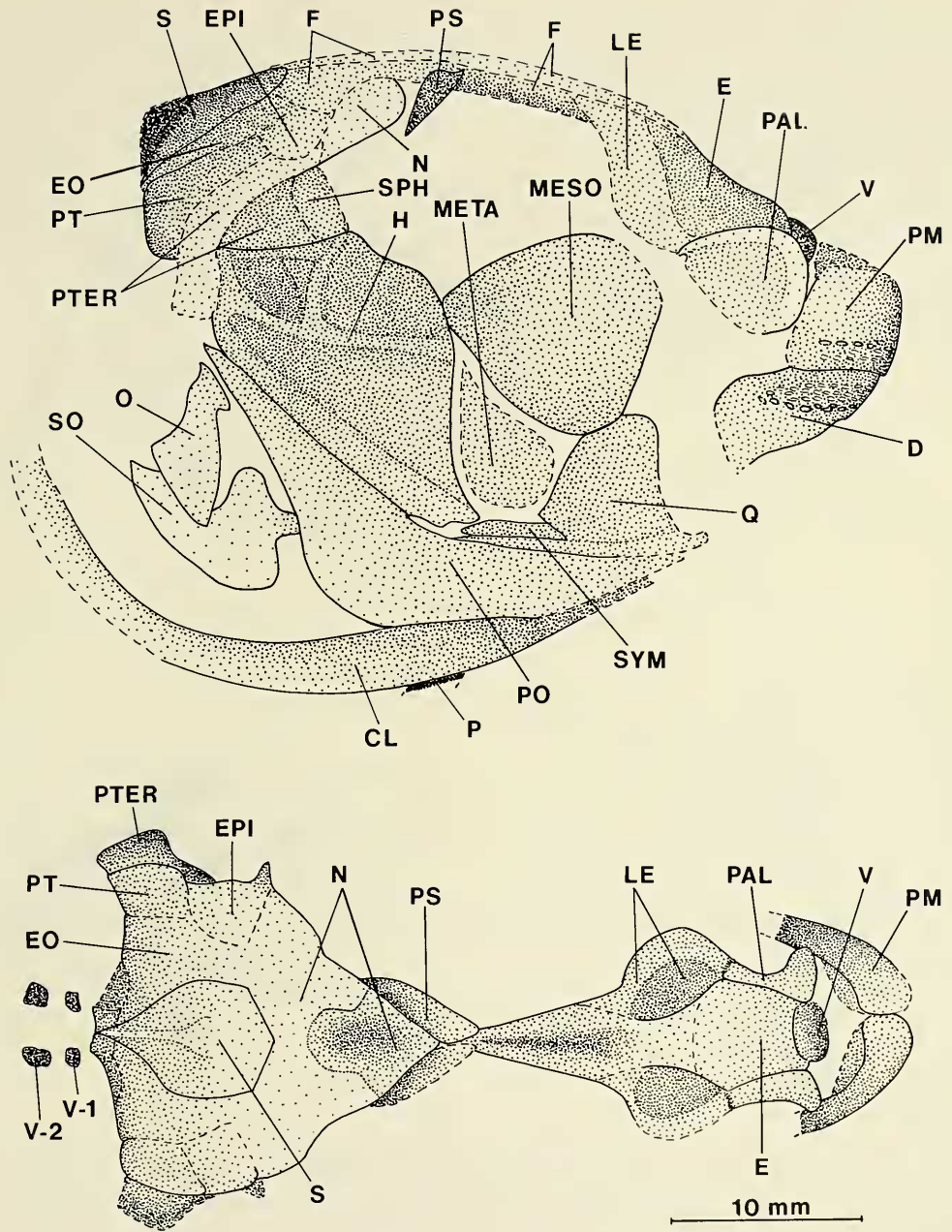


Fig. 5. *Triodon antiquus*, same specimen as Fig. 1, reconstruction of right lateral (above) and dorsal surfaces of skull (frontals missing). See legend for Fig. 6 for explanation of abbreviations of names of bones.

cent species slightly overlie the anterior edge of the supraoccipital, exoccipitals, and epiotics, are both missing. The region of the neurocranium underlying the frontals ap-

pears to be more heavily pyritized from the level of the front of the supraoccipital, epiotics, and exoccipitals to the pterosphenoids, while between the pterosphenoids and



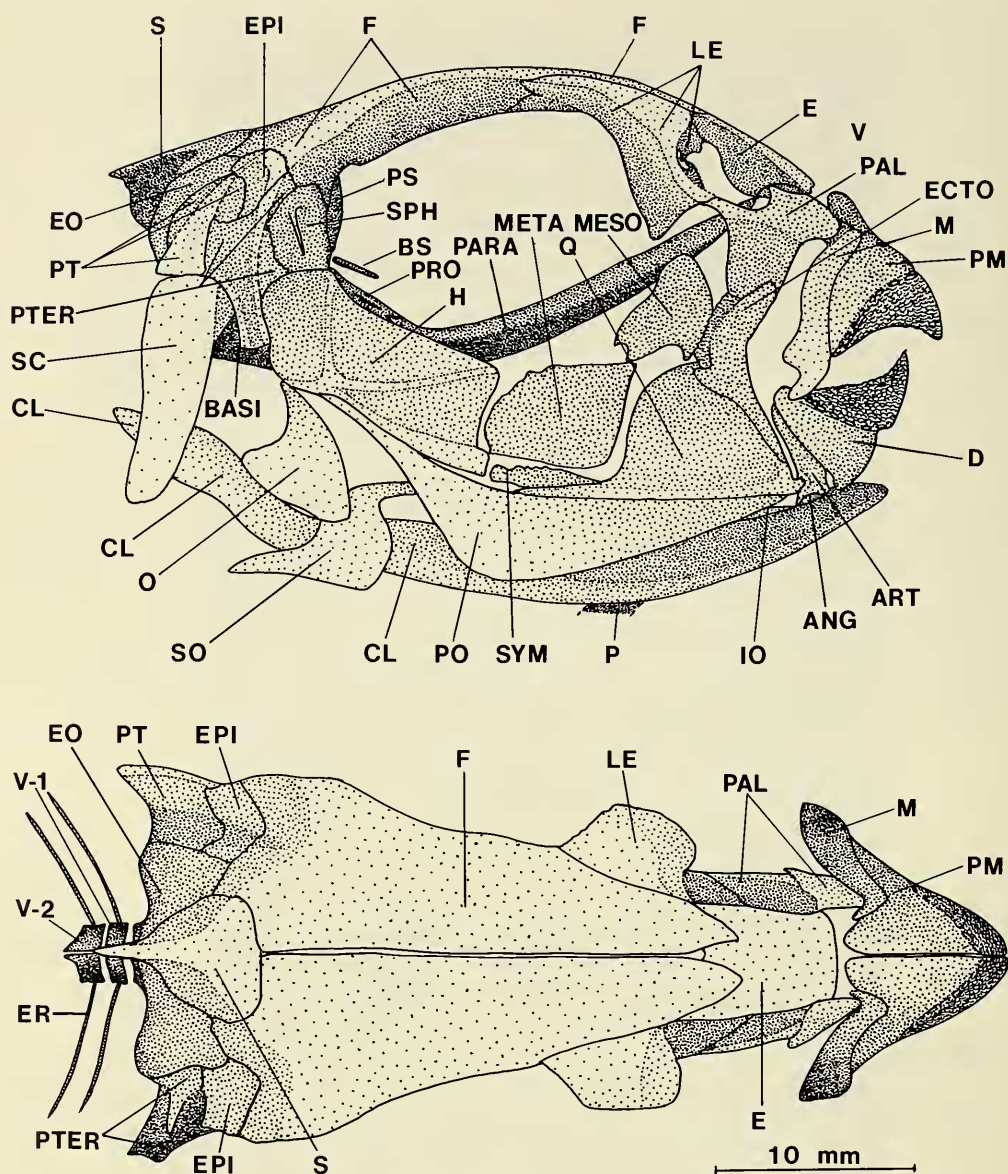


Fig. 6. *Triodon macropterus*, AMS I 25802-006, 103 mm SL, Queensland, Australia, right lateral (above) and dorsal views of skull (with posttemporal on right side removed in the dorsal view to expose the underlying pterotic. Abbreviations for the names of bones: ANG—angular; ART—articular; BO—basioccipital; BS—basisphenoid; C—coracoid; CL—cleithrum; D—dentary; E—ethmoid; ECTO—ectopterygoid; EO—exoccipital; EPI—epiotic; ER—epipleural rib; F—frontal; H—hyomandibular; IO—interopercle; LE—lateral ethmoid; M—maxilla; MESO—mesopterygoid; META—metapterygoid; N—neurocranium; O—opercle; P—pelvis; PAL—palatine; PARA—parasphenoid; PM—premaxilla; PO—preopercle; PRO—prootic; PS—pterosphenoid; PT—posttemporal; PTER—pterotic; Q—quadrate; S—supraoccipital; SC—supracleithrum; SPH—sphenotic; SO—subopercle; SYM—symplectic; V—vomer; V1—1st vertebra; V2—2nd vertebra.

the lateral ethmoids the mineralization probably is the impression of the ventromedial orbital flanges of the absent frontals. The massive ethmoid is relatively clearly indicated anteromedially on the skull, lateral to which are strong lateral ethmoids. At the lower anterior end of the ethmoid the anterior region of the underlying vomer can be seen, more so than is the case in *T. macropterus*, but probably mainly because of abrasion of the overlying ethmoid and the angle of view of the skull rather than any substantive difference between it and the Recent species.

Both premaxillae are much abraded, especially posterolaterally, and the medial region of the left premaxilla also is much worn away. However, it is clear that the premaxillae were separate bones, although closely articulated in the midline. The deeper parts of the articular area between the two premaxillae are not well enough exposed to determine if the articulation was strengthened by interdigitating bony processes from the apposed medial surfaces, as is the case in the Recent species of *Triodon* and of tetraodontids. A few individual small tooth elements are incorporated into the matrix of the bone of the premaxilla, but these teeth are better preserved in the dentary. The dentary is fully fused across the midline into a single piece with a gentle u-shaped curve along the internal edge but more acute along the front of the beak.

On the exposed external surface of the dentary the individual small teeth are clearly evident, being oblong with a slightly crenulated upper edge. This slight crenulation may be slightly better developed in *T. antiquus* than in the Recent species, but the teeth are much less crenulated than the deeply notched small teeth described for *T. cabindensis* (these small teeth are not apparent in *T. macrognathus*). The developmental centers for the individual small teeth form a row along the lower edge of the external tooth surface, as they do also on the

premaxillae. Much of the internal anteromedial surface of the dentary can be seen in ventral view, and the rear edges of a pair of large laterally elongate trituration teeth are evident. All of the jaw structures in the London Clay specimen are essentially similar to those of the Recent *T. macropterus*.

At the rear of the skull the condyle formed by the exoccipitals for articulation with the first vertebra is evident. The first several vertebrae are indicated by the much abraded left and right sides of the neural arches, the neural spines having been completely worn away.

Laterally on the skull the bones of the hyomandibular and opercular series are especially clear. The hyomandibular is large and strong. It bears a distinctive horizontal crest for muscle attachment. Another crest courses vertically upward from the horizontal crest to the anterior region of the place of articulation of the hyomandibular with the pterotic and sphenotic laterally (and presumably with the prootic internally), almost exactly as in the Recent *T. macropterus*. This size, shape, and pattern of crests is unique among tetraodontiforms, although many diodontids and some molids, but not tetraodontids, among the tetraodontids also have large and variously crested hyomandibulars (see illustrations throughout Tyler 1980). Another bone of relatively distinctive shape in both the London Clay skull of *T. antiquus* and in the Recent *T. macropterus* is the subopercle. It has a prominent anterior process from its anterior edge to behind the upper posterior edge of the preopercle where in the Recent species it connects by ligament to the posterior end of the interopercle. Such an anterior process is found among other tetraodontiforms only in diodontids and, in a more modified form, molids and is one of the few ways in which diodontids and molids are more similar to triodontids than are tetraodontids (Tyler 1980:342). The anterior process of the subopercle in *T. antiquus* differs from that in

*T. macropterus* by having its origin in about the middle of the anterior edge, rather than from the dorsal end as in *T. macropterus*, diodontids and, less clearly, molids.

Anteroventral to the hyomandibular the symplectic and the rear portion of the quadrate are clear. The articular and angular and the front end of the right quadrate are missing, leaving a large gap on this side between the posterolateral ramus of the dentary and the area of articulation with the quadrate. However, the anterior end of the quadrate is exposed in the matrix on the unprepared left side of the skull, and it has the typical triodontid (and tetraodontoid) appearance. The mesopterygoid in the London Clay specimen is much larger, and the metapterygoid much smaller (based on the space available for it between the hyomandibular and quadrate), than in the Recent *T. macropterus*. The palatine of the London Clay specimen is as large and strong to support the beak as the condition found in *T. macropterus* and most other tetraodontoids. Because the frontals are absent, the pterosphenoid (on the left side) is relatively clearly seen. The opercle and preopercle are well preserved but unremarkable.

The cleithrum is variously incomplete or not fully exposed at either end, but it was obviously an exceptionally long and sturdy structure, just as in the Recent *T. macropterus*. The cleithrum courses in a gentle arch from behind the level of the top of the opercle to under the level of the quadrate, where it is abraded away on both sides. Presumably this massive cleithrum continued forward to under the level of the dentary, as is uniquely the case in triodontids among the tetraodontiforms. The proximal ends of the two halves of the pelvis are present between the two cleithra under the posteroventral region of the preopercle, but the greater part of the length of the pelvis is broken off at the level of the ventral edges of the cleithra. The presence of a pelvis is unique to *Triodon* and the Eocene eoplectids among the tetraodontoids. In the 103 mm SL specimen

of *T. macropterus* the two halves of the pelvis are unfused but in close contact throughout their lengths. In larger specimens of *T. macropterus* the two halves of the pelvis fuse together in much of the posterior region, while the extreme posterior ends of the two halves still remain separate and end in a cartilaginous plug that may represent the remains of a rudimentary fin-ray element (Tyler & Matsuura 1981:65). In the region between the cleithra and preopercle in the London Clay specimen the remains of the hyoid arch are present, with the ceratohyal being especially clear.

Embedded in the matrix of the skull are scattered remains of scales, with a flat basal plate bearing an emarginate ridge with up to six distal points, relatively similar to the scales on the head of the Recent *T. macropterus*.

Our effort to interpret the otic bones of the London Clay specimen has led to the discovery of a posttemporal bone in the 103 mm SL specimen of *T. macropterus*. The posttemporal is present in all Balistoidei (with the possible exception of one species of highly specialized monacanthid; see Tyler & Matsuura 1981:60), and its supposed loss by all Tetraodontoidei was used by Tyler (1980:243) as one of the defining specializations for that suborder. In the two large adult cleared and stained specimens (391 and 463 mm SL) previously examined by Tyler, the area on the dorsal surface of the posterolateral region of the skull where posttemporals might be expected to be found on the basis of their occurrence in the Balistoidei, seemed fully consolidated into a single bone. Thus, the posttemporal was assumed to have been lost phylogenetically or incorporated indistinguishably into the pterotic in *Triodon* and all of the other Tetraodontoidei. However, in the 103 mm SL specimen of *T. macropterus* a large separate posttemporal overlies the dorsal and posterolateral surface of the pterotic. The posttemporal is prominent in both dorsal view, where it forms all of the posterolateral re-



gion of the skull, and in lateral view, where it forms a wedge-shaped buttress for articulation with the head of the supracleithrum. For purposes of clarifying the relationships of the posttemporal and the underlying pterotic, the posttemporal has been detached from the right side of the skull of the 103 mm specimen of *T. macropterus* and so illustrated.

In the London Clay specimen the pterotic is seen mainly on the left side of the skull, as a ventrally produced flange for support of the upper rear edge of the hyomandibular, just as in the Recent species (this flange is broken away on the right side). We believe that the bone just above this flange forming the posterolateral region of the skull in the London Clay specimen is the posttemporal, even though its articulations with the exoccipital medially, epiotic anteriorly, and pterotic ventrally are unclear.

The presence of a posttemporal in *Triodon* is one less way in which the Tetraodontoidei can be distinguished from the Balistoidei and one more way in which triodontids retain primitive balistoid features that have been lost by all other Tetraodontoidei.

### Conclusion

The similarity of the distinctive features of the skull and jaws of the Eocene *Triodon antiquus* with those of the Recent *T. macropterus* is assurance of the existence about 50 million years ago of a fish rather like the extant species, and argues for the retention of the fossil and Recent species in the same genus. The Triodontidae, the most primitive family of Tetraodontoidei other than the Eocene eoplectids, has been remarkably conservative in its anatomy since the Eocene, when its lineage separated from that of the other three Recent families of the suborder.

### Material

*Triodon macropterus* Lesson. Australian Museum (AMS) I 25802-006, 1 specimen, 103 mm SL, Queensland; California Acad-

emy of Sciences (CAS, specimen formerly at Stanford University (SU)) 13747, 1, 391 mm, Philippines; Academy of Natural Sciences (ANSP) 98917, 1, 463 mm, Japan.

*Triodon antiquus* Leriche. For materials that are relatively unabraded and intact, the measurement given for the premaxilla is its length and for the dentary is its greatest width across the posterolateral rami. Most materials, however, are severely abraded or fragmented, and the measurement is then the greatest dimension of the piece, which in the case of dentaries is still across the abraded rami if possible. United States National Museum of Natural History (USNM) 265387, 1 dentary, 10 mm, Popes Creek, Charles County, Maryland, Lower Eocene of Pamunkey Group, Nanjemoy Formation, the specimen described by Weems & Horman (1984:47). All of the following are in the British Museum (Natural History) (BM(NH)). From the London Clay Formation (Ypresian): P.62702, skull, 40 mm from front of jaws to rear of supraoccipital, Sheppey, Kent; P.52519, dentary, 10 mm, Sheppey; P.46696, front of dentary, 5 mm, Sheppey; P.28899, tooth-bearing fragment, 7 mm, Bognor Regis, Sussex. From the Wittering Formation (Lutetian): P.50857, tooth-bearing fragment, 7 mm, East Wittering, Sussex. From the Earnley Formation (Lutetian): P.38620, dentary, 11 mm, Southampton, Hampshire; P.22348, dentary, 10 mm, Southampton; P.28190, front of dentary, 7 mm, Southampton; P.51560, dentary, 11 mm, and incomplete right premaxilla, 7 mm, Yateley, Hampshire; P.25776-81, five dentaries, some incomplete, 4-7 mm, and one right premaxilla, 7 mm, Southampton. From the Bracklesham Group (unspecified Formation, Lutetian): P.26426, right premaxilla, 7 mm, Bracklesham Bay, Sussex. From the lower Barton Formation (Bartonian): P.12629, right premaxilla, 8 mm, and two fragments, 4-6 mm, Barton Clay, Barton, Hampshire; P.58456-8, a left premaxilla and two fragments of premaxilla, one left and one right, 6-7 mm,

Bed A3, Barton; P.15193, right premaxilla, 11 mm, and a 6 mm tooth-bearing fragment, Barton; P.14028, front of right premaxilla, 6 mm, lower Barton Clay, Barton. From the Bruxelles Formation (Lutetian): P.15726, front of dentary, 7 mm, Schaerbeek (Kattepoel), Belgium, specimen received from M. Leriche in 1931.

We have no explanation for the fact that of the identifiable disarticulated jaw parts in the BM(NH), all but three of the 14 Ypresian and Lutetian (older) specimens are dentaries, whereas all six of the Bartonian (younger) specimens are premaxillae. Presumably it needs no more explanation than the sampling error that also must be responsible for the fact that seven of the nine identifiable premaxillae are from the right side.

#### Acknowledgments

We are most grateful to Brian Gasson, Redhill, Surrey, for donating his London Clay *Triodon* skull to the British Museum (Natural History). We thank Richard Winterbottom, Royal Ontario Museum, and G. David Johnson, National Museum of Natural History, for presubmission comments on the manuscript, which was further improved by the reviews of Lance Grande, Field Museum of Natural History, and J. D. Stewart, Los Angeles County Museum of Natural History. John Paxton, Australian Museum, William Eschmeyer, California Academy of Sciences, and Eugenie Böhlke, Academy of Natural Sciences of Philadelphia are thanked for the loan of specimens. At the National Museum of Natural History we appreciate the photography of Chip Clark and the typing of Judy Lombardo and Diane Tyler.

#### Literature Cited

- Burgess, W., & H. R. Axelrod. 1974. Pacific marine fishes. Book 5. Fishes of Taiwan and adjacent waters. T.F.H. Publications, Neptune City, New Jersey, pp. 1111-1381.
- Casier, E. 1946. La faune ichthyologique de l'Ypresien de la Belgique. — Mémoires du Musée Royal d'Histoire Naturelle de Belgique 104:1-267.
- . 1960. Note sur la collection des poissons Paléocènes et Eocènes de l'Enclave de Cabinda (Congo). — Annales du Musée Royal du Congo Belge (Tervuren), A (Minéralogie, Géologie, Paléontologie), série 3 (Paléontologie) 1-2:1-47.
- . 1966. Faune ichthyologique du London Clay. British Museum (Natural History), 496 pp.
- Dartevelle, E., & E. Casier. 1943. Les poissons fossiles du Bas-Congo et des régions voisines (première partie). — Annales du Musée du Congo Belge (Tervuren), A (Minéralogie, Géologie, Paléontologie), série 3, 2(1):1-200.
- , & ———. 1949. Les poissons fossiles du Bas-Congo et des régions voisines (deuxième partie). — Annales du Musée du Congo Belge (Tervuren), A (Minéralogie, Géologie, Paléontologie), série 3, 2(2):201-256.
- , & ———. 1959. Les poissons fossiles du Bas-Congo et des régions voisines (troisième partie). — Annales du Musée Royal du Congo Belge (Tervuren), A (Minéralogie, Géologie, Paléontologie), série 3, 2(3):257-568.
- Gloerfelt-Tarp, T., & P. J. Kailola. 1984. Trawled fishes of southern Indonesia and northwestern Australia. Australian Development Assistance Bureau, 406 pp.
- Kyushin, K., K. Amaoka, K. Nakaya, & H. Ida. 1977. Fishes of Indian Ocean. Japan Marine Fishery Resource Research Center, 392 pp.
- , ———, ———, ———, Y. Tanino, & T. Senta. 1982. Fishes of the South China Sea. Japan Marine Fishery Resource Research Center, 333 pp.
- Leriche, M. 1905. Les poissons Éocènes de la Belgique. — Mémoires du Musée Royal d'Histoire Naturelle de Belgique 3:49-228.
- . 1906. Contribution à l'étude des poissons fossiles du nord de la France et des régions voisines. Mémoires de la Société Géologique du Nord (Lille) 5:1-430.
- . 1908. Les vertébrés du nummulitique de l'Aude. In L. Doncieux, ed., Catalogue descriptif des fossiles nummulitiques de l'Aude et de l'Herault, 2 partie. — Annales de Université de Lyon, nouvelle série 22:1.
- . 1919. Sur des poissons fossiles de la région côtière du Congo et sur la présence de l'Eocène dans cette région. — Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences (Paris) 169(10):479-481.
- . 1920. Note préliminaire sur des poissons nouveaux du Paléocène et de l'Éocène de la région côtière du Congo. — Revue Zoologique Africaine (Bruxelles) 8:80-86.

- Matsuura, K. 1985. *Triodon macropterus* Lesson. P. 748 in O. Okamura, ed., *Fishes of the Okinawa Trough and the adjacent waters*. Japan Fisheries Resource Conservation Association, 781 pp.
- Nolf, D. 1970. De geremaneerde Eocene visfauna in de basis van het Pleistoceen te Merelbeke.—*Natuurwetenschappelijk Tijdschrift (Gent)* 51(3–8):111–124.
- Smith, M. M. 1986. Triodontidae. P. 894 in M. M. Smith, & P. C. Heemstra, eds., *Smith's sea fishes*. Macmillan South Africa, Johannesburg, 1047 pp.
- Taverne, L., & D. Nolf. 1978. Troisième note sur les poissons des Sables de Ledé (Eocène Belge): les fossiles autres que les otolithes.—*Bulletin de la Société Belge de Géologie* 87(3):125–152.
- Tyler, J. C. 1962. *Triodon bursarius*, a plectognath fish connecting the Sclerodermi and Gymnodontes.—*Copeia* 1962(4):793–801.
- . 1967. A redescription of *Triodon macropterus* Lesson, a phyletically important plectognath fish.—*Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen*, series C 70(1):84–96.
- . 1980. Osteology, phylogeny, and higher classification of the fishes of the Order Plectognathi (Tetraodontiformes).—*National Oceanic and Atmospheric Administration Technical Report*, National Marine Fisheries Service Circular 434: 1–422.
- , & K. Matsuura. 1981. Comments on the osteology of balistoid fishes (Tetraodontiformes) with notes on the triodontid pelvis.—*Proceedings of the Biological Society of Washington* 94: 38–49.
- Weems, R. E., & S. R. Horman. 1983. Teleost fish remains (Osteoglossidae, Blochiidae, Scombridae, Triodontidae, Diodontidae) from the lower Eocene Nanjemoy Formation of Maryland.—*Proceedings of the Biological Society of Washington* 96:38–49.
- Winterbottom, R. 1974. The familial phylogeny of the Tetraodontiformes (Acanthopterygii: Pisces) as evidenced by their comparative myology.—*Smithsonian Contributions to Zoology* 155:1–201.
- (JCT) Office of the Director, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, U.S.A.; (CP) Department of Paleontology, British Museum (Natural History), London SW7 5BD, England.